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Phylogenetic placement of Sri Lankan goblin spiders (Araneae, Oonopidae): integrating new taxa and taxonomic implications

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Abstract

Sri Lanka harbours an exceptionally high diversity of goblin spiders (family Oonopidae), with 45 currently recognised species across 13 genera, of which 38 are endemic. In this study, we present a molecular phylogenetic analysis based on two nuclear ribosomal markers (*18S* and *28S* rRNA), incorporating 28 species from eight genera: *Aprusia*, *Brignolia*, *Ischnothyreus*, *Opopaea*, *Orchestina*, *Pelicinus*, *Silhouettella*, and *Xestaspis*. These taxa were analysed in the context of the existing global phylogeny, enabling both regional and broader evolutionary comparisons. Our results reveal that several genera, particularly *Brignolia*, *Opopaea*, and *Ischnothyreus*, are paraphyletic, highlighting the need for taxonomic revision. Endemic clades such as *Aprusia*, *Brignolia*, and *Xestaspis* show strong evidence of recent, within-island speciation and microendemism. The genus *Orchestina* is recovered as monophyletic, with Sri Lankan species forming a distinct clade. The findings support the hypothesis that reduced body sclerotisation is a plesiomorphic trait in oonopids. Overall, the study underscores the exceptional microendemism and evolutionary distinctiveness of Sri Lanka's oonopid fauna, likely driven by both ecological isolation and in situ speciation. However, given the incomplete representation of Indian and Southeast Asian taxa, and limited molecular sampling, further studies incorporating broader taxon and gene sampling are needed to fully resolve the origins and diversification of this ecologically important spider family.

Key Words

Araneae, Biogeography, Ceylon, Phylogenetics, short-range endemics

Introduction

Short-range endemic species are important for understanding both local biodiversity and broader biogeographic patterns (Harvey et al. 2011). Compared to more widespread and less habitat-specific invertebrates, they offer greater potential to reveal phylogeographic patterns and the influence of historical and present-day landscape processes (Harvey et al. 2011). They might be more susceptible to extinction (Mammola et al. 2018) due to climate change (Harvey and Dong 2023), agroforestry, urbanisation and pollution (Branco and Cardoso 2020). Generally, goblin spiders (Araneae: Oonopidae), which are considered short-range endemics with very restricted distributions, and may prove to be important indicator taxon for monitoring the effects of climate change and other threats on forest habitats (Baehr 2011).

Goblin spiders, currently include over 1978 described species in 115 genera (World Spider Catalog 2025). Members of this family are small (1–4mm), ecribellate, haplogyne (Jocqué and Dippenaar-Schoeman 2006), free hunting spiders that live in leaf litter, canopy, under stones, rocks, tree barks or even within buildings (Fannes et al. 2008; Grismado et al. 2011; Thoma et al. 2014). Goblin spiders are usually yellowish, orange or reddish-brown (Fig. 1), although some species can be whitish or pink (Saaristo 2001; Eichenberger et al. 2012). Although small in size, they exhibit a remarkable diversity of morphological characters (Platnick and Brescovit 1995; Fannes and Jocqué 2008; Platnick and Dupérré 2009a, b; Baehr and Ubick 2010; Baehr et al. 2010; Platnick and Dupér-

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Figure 1. A–D. Live goblin spiders, genus: *Xestaspis* sp. photo credit: SPB.

ré 2010a, b; Ubick and Griswold 2011; Brescovit et al. 2012a, b; Platnick and Berniker 2014; Platnick and Berniker 2015; Tong and Li 2015).

To date, thirteen genera of goblin spiders have been reported in Sri Lanka: *Aprusia* Simon, 1893 (Grismado et al. 2011; Ranasinghe and Benjamin 2018a), *Brignolia* Dumitrescu & Georgescu, 1983 (Platnick et al. 2011; Ranasinghe and Benjamin 2016a), *Camptoscaphiella* Caporiacco, 1934 (Baehr and Ubick 2010), *Cavisternum* Baehr, Harvey & Smith, 2010 (Ranasinghe and Benjamin 2018b), *Gamasomorpha* Karsch, 1881 (Eichenberger et al. 2012), *Grymeus* Harvey, 1987 (Ranasinghe and Benjamin 2018b), *Ischnothyreus* Simon, 1893, *Opopaea* Simon, 1892 (Platnick and Dupérré 2009), *Orchestina* Simon, 1882 (Ranasinghe and Benjamin 2025), *Pelicinus* Simon, 1892 (Ranasinghe and Benjamin 2018b), *Silhouettella* Benoit, 1979 (Ranasinghe and Benjamin 2018b), *Xestaspis* Simon, 1885 (Eichenberger et al. 2012; Ranasinghe and Benjamin 2016b) and *Xyphinus* Simon, 1893 (Ranasinghe and Benjamin 2016c), which includes 45 Oonopidae species, highlighting the diversity of the family on the island. Large continental islands such as Sri Lanka, where faunal assemblages are shaped by both recent colonisation from the mainland and long-term in situ diversification (Mayr 1947) remain relatively understudied in terms of their evolutionary dynamics (Beenaerts et al. 2010; Benjamin 2010; Pyron et al. 2013; Karunarathna et al. 2019; Meegaskumbura et al. 2019; Sudasinghe et al. 2020; Perera and Suranjanfernando 2024). Within this context, the family Oonopidae (goblin spiders) presents a compelling study group. The first molecular phylogeny of Oonopidae by Busschere et al. (2014), based on ribosomal RNA sequences from 37 genera, laid the groundwork for understanding the global diversity of this family. Field surveys across more than 100 localities have revealed that many of these species exhibit highly restricted distributions, some occurring at only a few sites, while others are known from a single forest patch and are absent even in the immediate surrounding forests (Ranasinghe and Benjamin 2016a, b, c, 2018a, b). These patterns highlight the significance of exploring the phylogenetic relationships of Sri Lanka's short-range endemic oonopids. Incorporating these taxa into a broader molecular framework will not only enhance the global phylogeny of the group but also provide critical insights into the evolutionary mechanisms driving microendemism on continental islands.

In this study, we present the first phylogeny of Sri Lankan goblin spiders and investigate the relationships of these short-range endemic species in the island to better understand how they contribute to the global diversity of the group (Busschere et al. 2014).

Methodology

Taxon Sampling

Specimens were collected from the natural forest of major climatic-physiographic zones of Sri Lanka (Pethiyagoda and Manamendra-Arachchi 1998), i.e. Central Mountain Range, Knuckles Range, Low Country wet zone and the dry zone, with the aim of maximizing the number of species collected (Fig. 2). Locations are listed alphabetically by provinces and districts in Appendix 1 (extended version of Batuwita and Benjamin 2014). Specimens were collected by sifting litter and leaving the residue overnight in a Winkler extractor or by hand sorting the residue. The collected specimens were preserved in 100% ethanol. The preserved specimens were examined using an Olympus SZX 7 stereomicroscope and identified up to generic level using recently published international revisionary works of Oonopidae (Platnick and Dupérré 2009; Baehr and Ubick 2010; Harvey and Smith 2010; Grismado et al. 2011; Platnick et al. 2011; Eichenberger et al. 2012; Henrard and Jocqué 2012; Platnick et al. 2012a, b).

DNA Extraction, amplification, purification and sequencing

Genomic DNA was extracted from 100% ethanol-preserved leg tissue using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacture's protocol. Initially, Polymerase chain reactions (PCR) were carried out using 10 primer pairs (Suppl. material 1: table S1) for 43 DNA samples (Suppl. material 1: table S2). However, the amplification of *16S*, *CO1* and *H3* fragments was only partially successful. Thus, four promising primer pairs (18Sa2.0/9R (650 bp), 18S3F/18Sbi (850 bp) 18S1F/18S5R (820 bp) and 28SZX/28SC (1200 bp) for three overlapping regions of *18S* and partial fragment of *28S* were selected for further PCRs. PCR was performed with an initial denaturation at 95 °C for 2'30", then 35 cycles started with denaturation at 95 °C (30"), annealing step of 30" 18Sa2.0/9R: 48 °C, 18S3F/18Sbi and 18S1F/18S5R: 56 °C, 28SZX/28SC: 48.5 °C and extension at 72 °C for 1'30" for 35 cycles. The PCR reaction mixture (20 µl) included Gotaq DNA Polymerase, 5× colorless Gotaq Flexi Buffer, Magnesium Chloride 25 mM, dNTP Mix (Promega Corporation, Madison, USA) and undiluted DNA template. PCR for older specimens was carried out using the Qiagen Multiplex PCR' kit (Qiagen, Hilden, Germany) in total reaction mixes of 20 µL, including 2 µL of undiluted DNA template, 1.6 µL of each primer (10 pM /mL), 2 µL of 'Q Solution' and 10 µL of the 'Multiplex PCR Master Mix', containing hot start TaqDNA polymerase and buffers. However, contrary to the manufacture's protocol the PCR reactions were not multiplexed, but run individually (Dimitrov et al. 2012; Huber et al. 2014). Thermal cycling was performed on a MyCycler (Biorad, California, USA). PCR products were visualized by 1% agarose gel in 1× TBE buffer. Bands were visually characterized as either weak or strong based solely on brightness. Strong bands were then purified using the QIAquick PCR Purification Kit (Qiagen). The weak bands were purified using the Illustra ExoProStar (GE Healthcare, UK) PCR clean-up system, according to manufacturer's protocol. All purified PCR products were Sanger sequenced in both direction by MACROGEN (Seoul, South Korea).

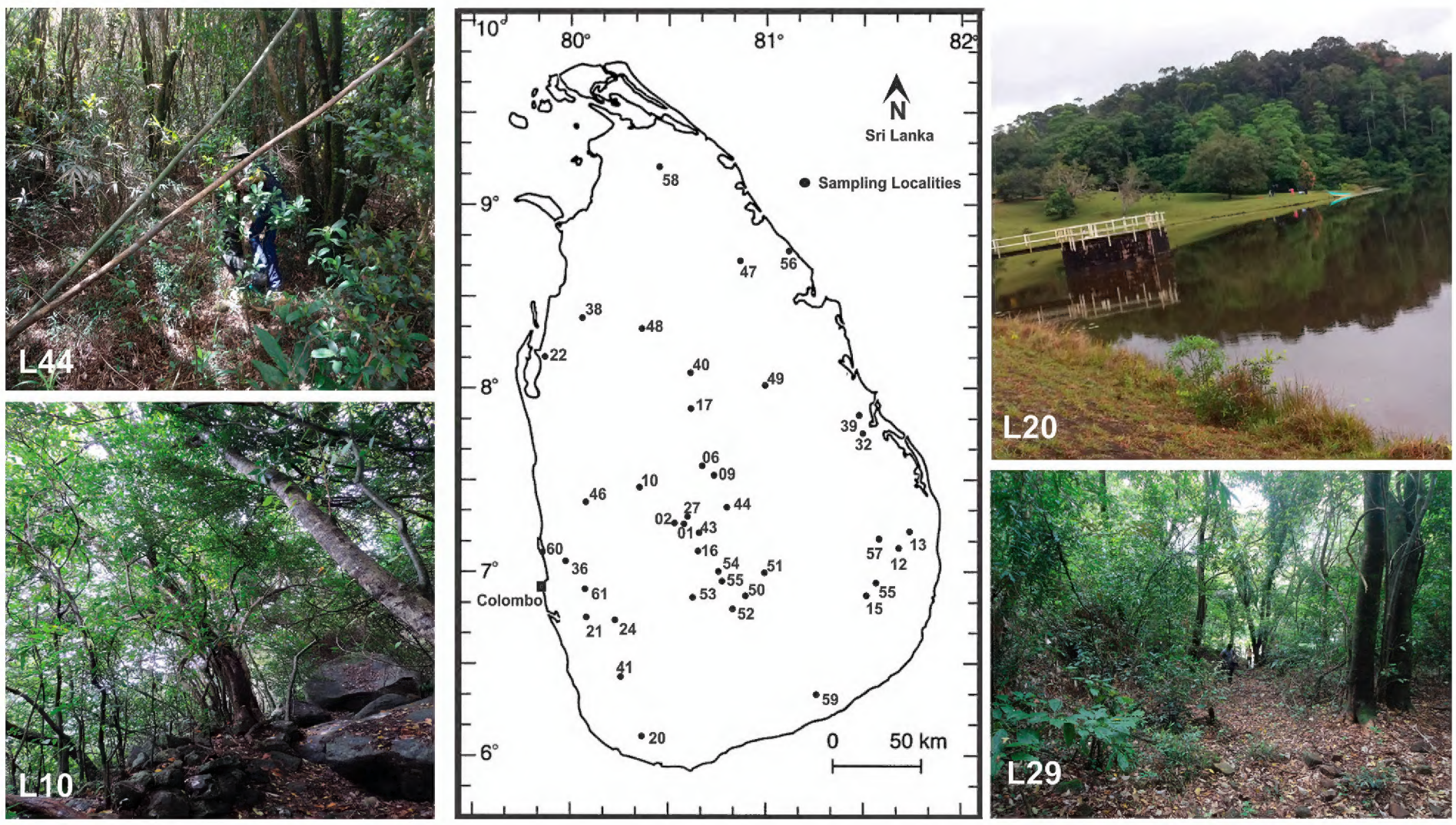

Figure 2. Sampling localities around Sri Lanka; L44: Knuckles forest reserve, L10: Ethagala forest, L20: Hiyare; L29: Meemure.

Sequence editing, alignment and phylogenetic tree construction

Sequences were edited and assembled using Geneious 6.1.5 software package (Kearse et al. 2012). Sequence alignment was done by Geneious 6.1.5 software using default parameters and then further refined and edited manually if needed using Mesquite (version 3.04; Maddison and Maddison 2011). Three data matrixes were assembled for analysis, *18S* (1796 bp), *28S* (1123 bp) and a concatenated *18S+28S* alignment. The concatenated *18S + 28S* matrix was 2782 bp in length. Maximum likelihood (ML; Felsenstein 1973) searches were performed in IQ-TREE version 1.6.12 (Nguyen et al. 2015) under the (GTR+F+I+G4) model of nucleotide substitution that was inferred as the best-fit model by ModelFinder (Kalyaanamoorthy et al. 2017). A total of 1000 ultrafast bootstrap (Hoang et al. 2018) replicates were done to assess branch supports.

Additional sequences of the Oonopidae *18S* region (n=111) and *28S* region (n=57) were obtained from GenBank (ncbi.nlm.nih.gov), and the whole dataset was assembled and aligned using the Mesquite software package (version 2.72; Maddison and Maddison 2011). Final analyses included 154 taxa representing 40 genera with a worldwide distribution (142 ingroup and 12 outgroup). The ingroup consisted of Oonopidae taxa and the outgroups were representatives of Dysderidae, Orsolobidae and Segestriidae. Representative Filistatidae and Liphistiidae taxa were used to root the tree (Busschere et al. 2014).

Results

We present a phylogenetic analysis based on two nuclear ribosomal loci (*18S* and *28S* rRNA), resolving the relationships among 43 goblin spider taxa from Sri Lanka. The dataset includes representatives from the genera *Aprusia*, *Brignolia*, *Camptoscaphiella*, *Ischnothyreus*, *Opopaea*, *Orchestina*, *Pelicinus*, *Silhouettella*, and *Xestaspis*. These taxa were integrated into a global phylogenetic framework (now consisting of 154 taxa representing 40 genera) with a worldwide distribution (142 ingroup and 12 outgroup taxa). This includes representatives of four families in the superfamily Dysderoidea: Dysderidae, Oonopidae, Orsolobidae, and Segestriidae, as well as the three subfamilies of Oonopidae: Oonopinae, Orchestininae, and Sulsulinae (as in Busschere et al. 2014).

Results from molecular analyses based on the *18S*, *28S*, and combined *18S+28S* datasets suggest that the family Oonopidae is monophyletic, supporting the findings of previous studies (Busschere et al. 2014). The genus level relationships within Oonopidae are well resolved in our analysis and largely align with morphologically defined groups, with a few exceptions. In contrast to previous works (Busschere et al. 2014), the genera *Aprusia*, *Camptoscaphiella* and *Xestaspis* are included here for the first time, while multiple species now represent *Brignolia* and *Pelicinus*. Moreover, monophyletic clades were recovered for the genera *Xestaspis*, *Escaphiella*, *Orchestina*, *Pelicinus*, and *Neotrops*. In contrast, *Brignolia*, *Opopaea*, *Aschnaoonops*, *Paradysderina*, *Unicorn*, and *Silhouettella* were not resolved as monophyletic in any of the analyses. In the updated global phylogeny, the Sri Lankan taxa exist in five distinct clades (Fig. 3), reflecting both multiple colonization and localized radiations within the island.

1. *Brignolia* and *Opopaea* clade

The genus *Brignolia* is well represented in all analyses including sixteen species for the combined analysis (Fig. 3). A well-supported *Brignolia* + *Opopaea* clade was recovered. However, neither genera are monophyletic. *Brignolia ondaatjei* is sister to Sri Lankan *Opopaea spinosiscorona* (Fig. 3). This group is well supported. Further, *B. ambigua*, *B. carlmulleri* and *B. shyami* formed a separate group. *B. ambigua* appeared as a sister to the other two species. This group is sister to *B. meemure* and *B. sinharaja*. *B. ratnapura* together with *B. parumpunctata* formed the next group. In the *18S+28S* concatenated analysis, all *Brignolia* species together with *Opopaea* species are sister to *O. apicalis* from the Galapagos, Ecuador (Fig. 3). However, *Opopaea* from Sri Lanka form a group separate from Australian, South American and African *Opopaea*. Thus, this study suggests that both genera need to be redefined in morphological terms.

2. *Xestaspis* clade

The character combination that defines *Xestaspis* is the reddish brown, well-sclerotised scuta, spineless legs, sternum with radial furrows and the presence of a palpal bulb that is not fused with the cymbium (Eichenberger et al. 2012). *Xestaspis* is included for the first time in a phylogenetic analysis of goblin spiders. It forms a well-supported clade (Fig. 3). Four species were included *Xestaspis kandy*, *X. nuwaraeliya*, *X. padaviya* and *X. pophami*. Here, *X. padaviya* is sister to all other *Xestaspis* species. *Xestaspis* is sister to *Prethopalpus tropicus* of Australia (Fig. 3).

3. *Silhouettella* and *Pelicinus* clade

The genera *Silhouettella* together with *Pelicinus* form sister groups in the combined analysis (Fig. 3). Both genera have quite similar secondary genital organs. However, *Pelicinus* differs by having conspicuously longer and slender spineless legs and large, oval-shaped operculae (Saaristo 2001). This clade consists of *P. marmoratus*, *P. snooky* and *P. tumpy*. They are sister to *Silhouettella snippy* and *S. saaristoi*.

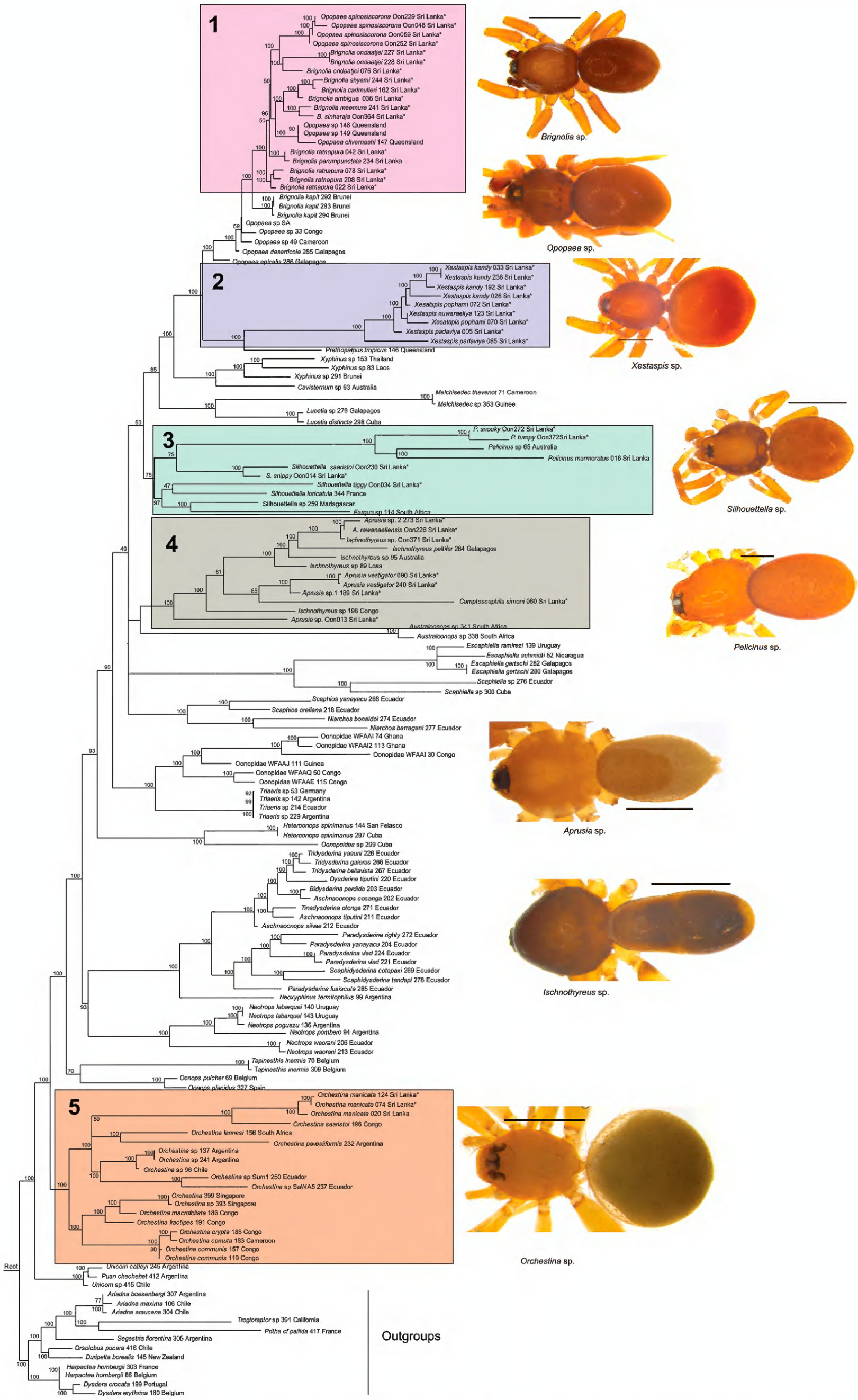
1
Opopaea spinosiscorona Oon229 Sri Lanka*
Opopaea spinosiscorona Oon048 Sri Lanka*
Opopaea spinosiscorona Oon059 Sri Lanka*
Opopaea spinosiscorona Oon252 Sri Lanka*
Brignolia ondaatjei 227 Sri Lanka*
Brignolia ondaatjei 228 Sri Lanka*
Brignolia ondaatjei 076 Sri Lanka*
Brignolia shyami 244 Sri Lanka*
Brignolia carlmulleri 162 Sri Lanka*
Brignolia ambigua 036 Sri Lanka*
Brignolia meemure 241 Sri Lanka*
B. sinharaja Oon364 Sri Lanka*
Opopaea sp 148 Queensland
Opopaea sp 149 Queensland
Opopaea olivernashi 147 Queensland
Brignolia ratnapura 042 Sri Lanka*
Brignolia parumpunctata 234 Sri Lanka
Brignolia ratnapura 078 Sri Lanka*
Brignolia ratnapura 208 Sri Lanka*
Brignolia ratnapura 022 Sri Lanka*
Brignolia kapit 292 Brunei
Brignolia kapit 293 Brunei
Brignolia kapit 294 Brunei
Opopaea sp SA
Opopaea sp 33 Congo
Opopaea sp 49 Cameroon
Opopaea desertiocla 285 Galapagos
Opopaea spicalis 286 Galapagos
Brignolia sp.
Opopaea sp.
2
Xestaspis kandy 033 Sri Lanka*
Xestaspis kandy 236 Sri Lanka*
Xestaspis kandy 192 Sri Lanka*
Xestaspis kandy 026 Sri Lanka*
Xesatspis pophami 072 Sri Lanka*
Xestaspis nuwaraeliya 123 Sri Lanka*
Xesatspis pophami 070 Sri Lanka*
Xestaspis padaviya 005 Sri Lanka*
Xestaspis padaviya 085 Sri Lanka*
Prethopaipus tropicus 146 Queensland
Xestaspis sp.
Xyphinus sp 153 Thailand
Xyphinus sp 83 Laos
Xyphinus sp 291 Brunei
Cavisternum sp 63 Australia
Melchisedec thevenot 71 Cameroon
Melchisedec sp 353 Guinee
Lucetia sp 279 Galapagos
Lucetia distincta 298 Cuba
3
P. snooky Oon272 Sri Lanka*
P. tumpy Oon372Sri Lanka*
Pelicinus sp 65 Australia
Pelicinus marmoratus 016 Sri Lanka
Silhouettella saaristoi Oon230 Sri Lanka*
S. snippy Oon014 Sri Lanka*
Silhouettella tiggy Oon034 Sri Lanka*
Silhouettella loricatula 344 France
Silhouettella sp 259 Madagascar
Fargua sp 114 South Africa
Silhouettella sp.
4
Aprusia sp. 2 273 Sri Lanka*
A. rawanaellensis Oon225 Sri Lanka*
Ischnothyreus sp. Oon371 Sri Lanka*
Ischnothyreus peltifer 284 Galapagos
Ischnothyreus sp 95 Australia
Ischnothyreus sp 89 Laos
Aprusia vestigator 090 Sri Lanka*
Aprusia vestigator 240 Sri Lanka*
Aprusia sp.1 189 Sri Lanka*
Camptoscaphila simoni 060 Sri Lanka*
Ischnothyreus sp 198 Congo
Aprusia sp. Oon013 Sri Lanka*
Pelicinus sp.
Australoonops sp 341 South Africa
Australoonops sp 338 South Africa
Escaphiella ramirezi 139 Uruguay
Escaphiella schmidti 52 Nicaragua
Escaphiella gertschi 282 Galapagos
Escaphiella gertschi 280 Galapagos
Scaphiella sp 276 Ecuador
Scaphiella sp 300 Cuba
Scaphios yanayacu 268 Ecuador
Scaphios orellana 218 Ecuador
Niarchos bonaldoi 274 Ecuador
Niarchos barragani 277 Ecuador
Oonopidae WFAAI 74 Ghana
Oonopidae WFAAI2 113 Ghana
Oonopidae WFAAI 30 Congo
Oonopidae WFAAJ 111 Guinea
Oonopidae WFAAQ 60 Congo
Oonopidae WFAAE 115 Congo
Triaeris sp 53 Germany
Triaeris sp 142 Argentina
Triaeris sp 214 Ecuador
Triaeris sp 229 Argentina
Aprusia sp.
Heteroonops spinimanus 144 San Felasco
Heteroonops spinimanus 297 Cuba
Oonopoides sp 299 Cuba
Tridysderina yasuni 226 Ecuador
Tridysderina galeras 266 Ecuador
Tridysderina bellavista 267 Ecuador
Dysderina tiputini 220 Ecuador
Bidysderina perdido 203 Ecuador
Aschnaoonops cosanga 202 Ecuador
Tinadysderina otonga 271 Ecuador
Aschnaoonops tiputini 211 Ecuador
Aschnaoonops silvae 212 Ecuador
Paradysderina nighty 272 Ecuador
Paradysderina yanayacu 204 Ecuador
Paradysderina vlad 224 Ecuador
Paradysderina vlad 221 Ecuador
Scaphidysderina cotopaxi 269 Ecuador
Scaphidysderina tandapi 278 Ecuador
Paradysderina fusiscuta 265 Ecuador
Neoxyphinus termitophilus 99 Argentina
Ischnothyreus sp.
Neotrops labarquei 140 Uruguay
Neotrops labarquei 143 Uruguay
Neotrops poguazu 136 Argentina
Neotrops pombero 94 Argentina
Neotrops waorani 206 Ecuador
Neotrops waorani 213 Ecuador
Tapinesthis inermis 70 Belgium
Tapinesthis inermis 309 Belgium
Oonops pulcher 69 Belgium
Oonops placidus 327 Spain
5
Orchestina manicata 124 Sri Lanka*
Orchestina manicata 074 Sri Lanka*
Orchestina manicata 020 Sri Lanka
Orchestina saaristoi 196 Congo
Orchestina fannesi 156 South Africa
Orchestina pavesiiformis 232 Argentina
Orchestina sp 137 Argentina
Orchestina sp 241 Argentina
Orchestina sp 96 Chile
Orchestina sp Sum1 250 Ecuador
Orchestina sp SaWA5 237 Ecuador
Orchestina 399 Singapore
Orchestina sp 393 Singapore
Orchestina macrofoliata 186 Congo
Orchestina fractipes 191 Congo
Orchestina crypta 185 Congo
Orchestina comuta 183 Cameroon
Orchestina communis 157 Congo
Orchestina communis 119 Congo
Orchestina sp.
Root
Unicom calfayi 245 Argentina
Puan chechehet 412 Argentina
Unicom sp 415 Chile
Ariadna boesenbergi 307 Argentina
Ariadna maxima 106 Chile
Ariadna araucana 304 Chile
Trogloraptor sp 391 California
Pritha cf pallida 417 France
Segestria florentina 305 Argentina
Orsolobus pucara 416 Chile
Duripelta borealis 145 New Zealand
Harpactea hombergii 303 France
Harpactea hombergii 86 Belgium
Dysdera crocata 199 Portugal
Dysdera erythrina 180 Belgium
Outgroups

Figure 3. Phylogenetic relationships of Oonopidae and related families based on concatenated *18S+28S* sequence data (2782 bp), including 154 taxa (142 ingroup), species of Orsolobidae, Dysderidae, Segestriidae included as outgroups. Numbers on branches indicate bootstrap proportions > 40% from 1000 replicates. Sri Lankan endemics are indicated with an asterisk (*).

4. *Aprusia*, *Camptoscaphiella* and *Ischnothyreus* clade

The South Asian goblin spider genus *Aprusia* is characterised by a unique combination of characters, such as the relatively small to medium-sized dorsal scutum, the presence of strong spines on leg I and II, the anteriorly directed receptaculum and the male palpal bulb fused to cymbium and a small, slightly sclerotised embolus (Grismado et al. 2011). According to the combined analysis *Aprusia* and *Ischnothyreus* together with *Camptoscaphiella* form a well-supported clade (Fig. 3). However, both *Aprusia* and *Ischnothyreus* are paraphyletic (only a single species of *Camptoscaphiella* is included in the current study). *Aprusia* sp. 2 is sister to *Ischnothyreus peltifer* from the Galapagos, albeit with low support. Further, *Aprusia vestigator* (Simon 1893) is sister to *Aprusia* sp. 1 (IFS_Oon_189). This clade is recovered as sister to Sri Lankan *Camptoscaphiella simoni*.

5. *Orchestina* clade

The soft-bodied goblin spider genus *Orchestina* includes canopy-dwelling jumpers that are easily identified by the elongated and enlarged fourth femora, H-shaped eye arrangement and enlarged male palpal tibia (Saaristo 2001; Henrard and Jocqué 2012). Three specimens form a well-separated branch. In the global analyses, it is represented by 19 specimens from different continents (Africa, Asia and South America). The three Sri Lankan *Orchestina* form a well-supported clade which is sister to the Congolese *Orchestina saaristoi* in all three analyses (Fig. 3, Suppl. materials 2, 3, fig. 2 in Ranasinghe and Benjamin 2025).

Tree-based species delimitation (Poisson tree processes model (Zhang et al. 2013)) for only Sri Lankan species for their individual *18S*, *28S*, and combined *18S+28S* trees showed above five distinct clustering pattern (shown as boxes in Fig. 4).

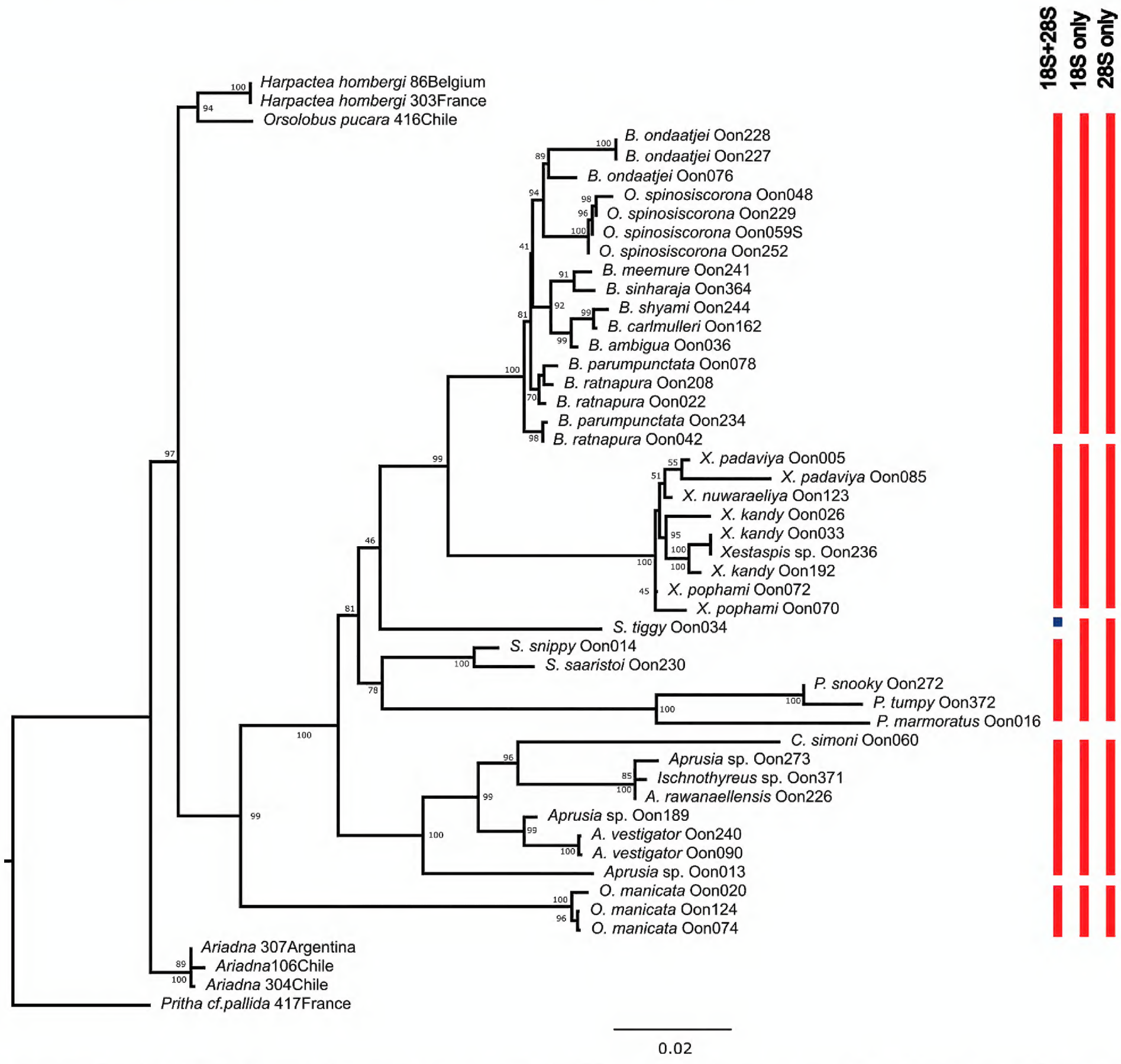

Figure 4. Tree-based Poisson tree processes model of species delimitation for Sri Lankan oonopids for their individual *18S*, *28S*, and combined *18S+28S* trees. Boxes indicate agreement between molecular species delimitation method and species assignment.

Discussion

The selection of genes for this study was guided by two main considerations. First, although we attempted to amplify fragments of *18S*, *28S*, *16S*, *CO*1 and *H3* for the sampled species, the most consistent and successful results were obtained for the ribosomal RNA genes *18S* and *28S*. Second, we prioritised compatibility with the existing global phylogeny of Busschere et al. (2014), necessitating the use of these same markers. However, the *18S* and *28S* genes evolve relatively slowly and are highly conserved across species, making them well-suited for examining deep evolutionary relationships (Koh et al. 2023; Xing et al. 2025; Fig. 4).

Although strong support for the monophyly of *Brignolia* + *Opopaea* has been previously reported (Busschere et al. 2014), both were recovered here as paraphyletic. This result contrasts with the current morphological hypothesis that both genera are monophyletic. The presence of the dorsal depression ("fenestra") on the palp was previously considered synapomorphic for both genera (Platnick and Dupérré 2009a). However, *Opopaea* differ from *Brignolia* by the presence of a distinct enlarged male palpal patella. Females of *Brignolia* and *Opopaea* are very similar in having a dorsal abdominal scutum that covers most of the abdomen. However, female *Brignolia* have a simple or twisted posterior genitalic tube that is absent in females of *Opopaea* (Platnick et al. 2011; Platnick et al. 2012a). In this study, *B. ratnapura* and *B. parumpunctata* formed a well-supported group. Platnick et al. (2011) stated that *B. ratnapura* might be the sister species of the pantropical *B. parumpunctata*, based on their genitalic structures. The two species share a rounded dorsal protrusion on the male palpal bulb (figs 12, 280 in Platnick et al. 2011) and a highly twisted posterior tube within the female genitalia (figs 71, 294 in Platnick et al. 2011). *B. carlmulleri* and *B. shyami* is recovered as sister species in the combined analysis. The presence of a triangular projection on the base of the endite (figs 4c, 17a, b in Ranasinghe and Benjamin 2016a), dorsally directed palpal tip and the rounded palpal tibia in males (figs 6a, 18a in Ranasinghe and Benjamin 2016a) are characters shared in both species. Further, males of *Opopaea*, *Prethopalpus*, *Camptoscaphiella* and *Malagiella* have a greatly enlarged palpal patella that originates sub-basally or medially from the femur (Platnick and Dupérré 2009; Baehr 2011; Baehr et al. 2013). The later genus was not included in this analysis.

Aprusia and *Ischnothyreus* together with *Camptoscaphiella* form a well-supported clade in the *18S* and the *18S*+ *28S* phylogeny (Fig. 3, Suppl. materials 2, 3). However, *Aprusia* and *Ischnothyreus* are both paraphyletic and needs further taxonomic attention. *Aprusia* resembles *Ischnothyreus* and *Camptoscaphiella* in eye arrangement, the shape of the abdominal scutum and the strong spination on legs I and II (Grismado et al. 2011). However, they differ in their copulatory organs. The copulatory orifice opens on the postepigastric plate in *Camptoscaphiella* and *Ischnothyreus*, while the opening is inconspicuous and located presumably in the epigastric furrow in *Aprusia* (Baehr and Ubick 2010; Grismado et al. 2011; Platnick et al. 2012a).

All analyses recovered a well-supported monophyletic *Orchestina* (same as in Busschere et al. 2014). Sri Lankan *Orchestina* species form a well-supported clade, sister to *O. saaristoi* from the Congo, whereas two specimens from Singapore form a different clade with *O. macrofoliata* Henrard & Jocqué, 2012 and *O. fractipes* Henrard & Jocqué, 2012 from the Congo. Sri Lankan *Orchestina* specimens are morphologically similar to *O. saaristoi* (figs 573–605, 607 in Henrard and Jocqué 2012; Ranasinghe and Benjamin 2025).

The genus *Silhouettella* is paraphyletic in the *18S* as well as the *18S*+*28S* combined phylogeny (Fig. 3, Suppl. material 2). In the combined analysis, *Silhouettella snippy* and *S. saaristoi* from Sri Lanka group together, while *Silhouettella* sp. from Madagascar is placed as sister to *Farqua* sp. from South Africa. However, *S. tiggy* from Sri Lanka is placed as sister to *Silhouettella loricatula* from France. According to the *18S* and *18S*+*28S* phylogeny, *Pelicinus* formed a well-supported clade (Fig. 3, Suppl. material 2). Two species of *Pelicinus* from Sri Lanka (*Pelicinus marmoratus* and *P. snooky*) group with *Pelicinus* sp. 65 from Australia. Previous morphological studies group *Pelicinus*, *Silhouettella*, *Lionneta* and *Grymeus* together and consider them members of the *Pelicinus* group (Burger 2011; Platnick et al. 2012b). Shared features include the "squiggled" shape of the globular appendix, the pore plate in front of the posterior receptaculum and the details of the anterior "paddle like sclerite" in the female genitalia (Burger 2011; Platnick et al. 2012b).

The *Dysderina*-group is a large morphologically defined group within Oonopidae, and several of these species form numerous well-supported groups within the Dysderina clade (Platnick and Dupérré 2011a, b). These phylogenetic relationships are consistent with those of Busschere et al. (2014). The addition of new data does not seem to have any effect (but see Graybeal 1998; Zwickl and Hillis 2002; Heath et al. 2008). However, as in previous studies, even this small, geographically restricted sample is not recovered as monophyletic.

According to the results of the combined analysis, the hypothesis that Oonopidae is monophyletic is supported. Further, many oonopid genera constitute natural groups. Further, most soft-bodied genera are basal within the Oonopidae. Busschere et al. (2014) suggested that a low degree of body sclerotisation is a plesiomorphic trait, with a higher degree of body sclerotization being considered a derived trait among Oonopidae. This hypothesis is supported by the present results. In addition, these results confirm the hypothesis that Orchestininae and Sulsulinae are basal oonopids. However, inclusion of absent genera in future studies will help obtain better resolution and form a definite conclusion.

Considering the distribution of 45 Sri Lankan species, 38 are endemic (Ranasinghe 2017). Among them, few showed island-wide distribution, while most showed restricted distribution and were found in only one, two or

three sites among more than hundred sampling localities. *B. ratnapura*, *B. parumpunctata*, *B. ambigua*, *X. kandy*, *X. padaviya*, *A. vestigator*, *O. spinosiscorona* showed widespread distribution, while soft bodied *O. manicata* was reported only from the island's central montane wet evergreen forests. Certain species were found only in confined areas such as *B. ondaatjei* is known only from two sites in the Badulla District (L 50, L 30; 990–1280 m). *B. carlmulleri* is known only from Hantane and Knuckles mountain ranges in the Kandy District (L 43, 44; 585–1240 m). *X. pophami* is reported only at two sites (L 17, L 9) in the Matale District and *X. nuwaraeliya* is reported at three sites (L 53, L 54, L 55; >1700 m) in the Nuwara Eliya District. *A. vankhedei* is recorded from Udawattakele FR and Dunumadalawa FR, secondary forests located within Kandy City (L 1, L 27; 580–600 m). *A. koslandensis* was found in a small forest patch between Koslanda-Beragala, Namunukula and Bandarawela (L 52, L 51, L 67; 1000–1800 m). *S. saaristoi* Labugama FR, Kalugala FR (L 61, L 41; 40–200 m). Meanwhile, most species were found only the type locality: *A. rawanaellensis* (Rawana Ella), *B. meemure* (L 29; 636 m), *B. shyami* (L 28), *Cavisternum bom* (Mandaitivu FR), *S. snippy* (L 17), *S. tiggy* (Corbett's Gap), *P. tumpy* (Mihinthale L 48), *P. snooky* (Ethagala FR, L 10), *Ischnothyreus chippy* (L 52) (see fig. 1 Ranasinghe and Benjamin 2016a, figs 6, 13 Ranasinghe and Benjamin 2016b, fig. 11 Ranasinghe and Benjamin 2018 a; fig. 21 Ranasinghe and Benjamin 2018b; fig. 5 Ranasinghe and Benjamin 2025).

It is premature to comment on the origin of Sri Lanka's goblin spider diversity as the Indian fauna is not well known. However, this study suggests that both ecology and evolution may be contributing factors in their evolution. Considering phylogenetic analysis and species distribution patterns, we can hypothesise that most of this diversity is generated through within-island speciation. This is seen in clades such as *Aprusia*, *Brignolia* and *Xestaspis*, which consist of closely related assemblages of more than two endemic species (Ranasinghe and Benjamin 2016a, b, 2018a, b, 2025). These species are narrow endemics with very restricted distribution and are not expected to be found outside of Sri Lanka. *Aprusia*, *Brignolia* and *Xestaspis* are morphologically revised, and Indian species are known and differ from Sri Lankan species (Baehr and Ubick 2010; Grismado et al. 2011; Platnick et al. 2011; Grismado 2023).

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Appendix 1

Sampled localities are listed below in alphabetical order of the Provinces and Districts in the extended version of Batuwita and Benjamin 2014.

Central Province, Kandy District

L 1: Dunumadalawa, 07°17'00"N, 80°37'49"E, 600 m, 22 April 2010, S. P. Benjamin and S. Batuwita.
L 2: Gannoruwa, 07°16'56.85"N, 80°35'57.2"E, 575 m, 25 November 2013, N. Athukorala et al.
L 7: Deenston, Knuclkes Range, 07°20'10"N, 80°51'31"E, 1120 m, disturbed forest, litter sieving, 19 January 2010, S. P. Benjamin and S. Batuwita.
L 16: Deltota, Loolcondera FR, 07°08'45"N, 80°41'53"E, 1480 m, 11 May 2010, leg. S. Batuwita and N. Athukorala; 13 July 2010, leg. S. P. Benjamin, S. Batuwita, litter.
L 19: Randenigala, Victoria Randenigala Rantabe sanctuary, 07°09'14"N, 80°54'12"E, 289 m, 11 May 2010, leg. S. Batuwita and N. Athukorala, litter.
L 27: Udawattakelle FR, 07°17'57"N, 80°38'29"E, 580 m, 29 December 2011, leg. S. P. Benjamin, litter.
L 29: Meemure, 7°25'51"N, 80°50'44"E, 636 m, 20 October 2014, leg. N. Athukorala, U.G.S.L. Ranasinghe and C. Clayton, litter.
L 43: Hantane FR, 07°14'57"N, 80°36'50"E, 585 m, 19 November 2013, leg. M. Rathnayake and I. Sandunika; 18 December 2013, N. Athukorala et al., litter.
L 44: Knuckles, Riverston, Site 02, 07°31'25"N, 80°44'20"E, 1240 m, 25 February 2015, leg. N. Athukorala, litter/pitfall trap.
L 70: Corbett's Gap, Knuckles range, 07°21'40"N, 80°50'00"E, 1360 m, 02 November 2010, S. P. Benjamin, S. Batuwita, litter.

Central Province, Matale District

L 6: Gammaduwa, Knuckles range, 18 September 2009, 900m, leg. S. P. Benjamin and S. Batuwita.
L 9: Riverston, Knuckles range, 07°31'42"N, 80°44'17"E, 1100 m, 02 December 2009, S. P. Benjamin and S. Batuwita.
L 17: NIFS Arboretum, 07°51'34"N, 80°40'28"E, 180 m, 27 April 2010, leg. S. P. Benjamin and S. Batuwita; 01 December 2011, leg. S. P. Benjamin et al.; 24 August 2010, leg. S. P. Benjamin and S. Batuwita; 23 July 2010, S. Batuwita, litter.

Central Province: Nuwara Eliya District

L 53: Hakgala Strict Natural Reserve, 6°54'40"N, 80°47'36"E, 1913 m, 22 January 2015, leg. S. P. Benjamin et al., litter.
L 54: Nuwara Eliya town, 06°46'N, 80°36'E, 1887 m, 14 February 2012, S. P. Benjamin and N. Athukorala.
L 55: Hakgala Natural Reserve, 6°55'52"N, 80°48'46"E, 1728 m, 20 January 2015, N. Athukorala and S. Ranasinghe.
L 71: Upcot, 06°46'N, 80°36'E, 14 February 2012, S. P. Benjamin, N. Athukorala, beating.

Eastern Province: Ampara District

L 57: Kokagala, 07°25'28"N, 81°3'27"E, 125 m, 09 February 2010, leg. S. P. Benjamin and S. Batuwita, litter.
L 66: Nuwaragala FR, 07°26'07.4"N, 81°31'58.8"E, 70 m, 19 May 2015, leg. N. Athukorala, litter.

North Central Province, Anuradhapura District

L 38: Wilpattu National Park, Maradanmaduwa, 08°22'30"N, 80°05'00"E, 200 m, 06 April 2011, S. Batuwita.
L 40: Kodigala Summit, 08°06'33"N, 80°39'16"E, 716 m, 28 June 2011, S. P. Benjamin et al.
L 47: Padaviya, 8°48'0"N, 80°45'0"E, 51 m, 10 January 2012, N. Athukorala.
L 48: Mihinthale, 8°21'10.60"N, 80°30'14.54"E, 06 July 2014, N. Athukorala and C. I. Clayton.

North Central Province, Polonnaruwa District

L 49: Parakrama Samudraya, 07°53'51"N, 80°59'14"E, 57 m, 01 December 2009, N. Athukorala.

North Western Province, Kurunagala District

L 10: Ethagala, 07°28'17"N, 80°22'30"E, 190 m, 20 August 2010, leg. S. Batuwita; 08 April 2015, S. P. Benjamin et al., litter.
L 46: Kankaniyamulla forest reserve, 7°21'32"N, 80°02'07"E, 24 September 2014, N. Athukorala.

North Western Province, Puttalam District

L 22: Wanathavilluwa, 08°10'15"N, 79 °52'30"E, 30 m, 24 May 2010, leg. N. Athukorala; 19 July 2010, leg. N. Athukorala, litter.

Sabaragamuwa Province, Kegalle District

L 28: Kurulukele FR, 07°14'12"N, 80°20'33"E, 250 m, 12 November 2014, leg. N. Athukorala, litter.

Southern Province, Hambantota District

L 59: Tissamaharama, 6°17'N, 81°17'E, 18 m, 02 February 2014, leg. C. Clayton, litter.

Southern Province, Galle District

L 20: Hiyare, Kombala-Kottawa FR, 06°03'30"N, 80°18'55"E, 80 m, 24–26 May 2016, leg. N. Athukorala, litter.

Uva Province, Badulla District

L 30: Ohiya, 06°50'32"N, 80°53'05"E, 1280 m, 30 August 2011, leg. S. P. Benjamin and N. Athukorala, litter.

L 50: Rawana Ella, forest around cave, 6°51'52.4"N, 81°03'01.3"E, 990 m, 31 December 2011, leg. S. P. Benjamin et al.; 27 June 2014, leg. N. Athukorala and S. Ranasinghe, litter.

L 51: Namunukulla, along Passara/Ella road, 6°52'N, 81°7'E, 1838 m, 22 January 2014, leg. S. P. Benjamin and N. Athukorala; 27 February 2015, leg. S. P. Benjamin, N. Athukorala, litter.

L 52: 189th mp, Between Koslanda and Beragala, 6°44'48.4"N, 80°57'56.3"E, 1370 m, 01 January 2012, S. P. Benjamin et al., litter.

L 67: Bandarawela, 6°50'59.5"N, 81°00'48.1"E, 1042 m, 31 December 2011, S. P. Benjamin et al., litter.

L 69: 18th mile post, Passara, Elle Road (B113), Mausagalla, 1337 m, 22 January 2014, Lat.6.9091, Long.81.1323, S. P. Benjamin, N. Athukorala, litter.

Uva Province, Monaragala District

L 55: Westminister Abbey, 07°02'42"N, 81°32'16"E, 120 m, 10 February 2010, leg. S. P. Benjamin and S. Batuwita, litter.

Western Province, Gampaha District

L 36: Pilikuttuwa, close to Yakkala, 07°03'53"N, 80°03'04"E, 50 m, litter sieving and under tree bark, 17 January 2011, S. Batuwita.

L 62: Pilikuttuwa, c L 41: Gurulu Bedda, Kalugala Forest reserve, 06°26'35"N, 80°14'52"E, 40 m, 10 January 2014, S. P. Benjamin, N. Athukorala.

L 60: Kadolkelle FR, 7°11'49"N, 79°50'35"E, 10 m, 24 September 2014, leg. N. Athukorala, litter.

L 61: Labugama, 6°51'17"N, 80°16'47"E, 25 September 2014, N. Athukorala, litter.

Supplementary material 1

Supplementary tables

Authors: U. G. S. L. Ranasinghe, Suresh. P. Benjamin
Data type: docx
Explanation note: **table S1.** Details of Primers used for PCR. table s2: Details of specimens used in the Phylogenetic analysis. Localities (L) are listed in the Appendix 1.
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Link: https://doi.org/10.3897/evolsyst.9.168533.suppl1

Supplementary material 2

Phylogenetic relationships of Oonopidae and related families based on concatenated *18S* sequence data (1796 bp), including 154 taxa (142 ingroup), Species of Orsolobidae, Dysderidae, Segestriidae as outgroups

Authors: U. G. S. L. Ranasinghe, Suresh. P. Benjamin
Data type: tif
Explanation note: Numbers on branches indicate bootstrap proportions > 40% from 1000 replicates. Sri Lankan endemics are indicated with an asterisk (*).
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Link: https://doi.org/10.3897/evolsyst.9.168533.suppl2

Supplementary material 3

Phylogenetic relationships of Oonopidae and related families based on concatenated *28S* sequence data (1123 bp), including 85 taxa (80 ingroup), Species of Orsolobidae, Dysderidae as outgroups

Authors: U. G. S. L. Ranasinghe, Suresh. P. Benjamin
Data type: tif
Explanation note: Numbers on branches indicate bootstrap proportions > 40% from 1000 replicates. Sri Lankan endemics are indicated with an asterisk (*).
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Link: https://doi.org/10.3897/evolsyst.9.168533.suppl3